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BIOLOGICAL BULLETIN

AN EXPERIMENTAL STUDY OF CONCRESCENCE IN THE EMBRYO OF CRYPTOBRANCHUS ALLEGHENIENSIS.¹

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I. INTRODUCTION.

The concrescence theory is an attempt to establish a universal law for the formation of the embryo. It is also an attempt to apply to conditions found in the vertebrates, a law having a wide range of validity in the invertebrates.

In its widest sense, concrescence may be defined as the building-up of the body of the embryo by the union along the median line, of parts that are previously laid down as separate bilateral foundations. The classical case is that of the leech (Whitman, '78), in which the entire body, excepting the head, is formed by concrescence.

In the vertebrates the formation of the nerve tube by the apposition of the neural folds, and the formation of the gastral mesoderm in two more or less distinct halves which later unite across the median line, come within the category of concrescence in this wide sense of the term. But the problem has usually been restricted to certain aspects of development intimately related to gastrulation. Thus, in the teleost the convergence² of the germ ring until its materials coalesce to form the posterior part of the embryo, has been regarded as a process of concrescence. A very similar process occurs, though less conspicuously, in the amphibian embryo.

¹ An abstract of this paper was read before the American Society of Zoologists at the meeting in Philadelphia, December 29, 1913.

² Since among authors there is no uniformity in the use of the words *convergence*, *confluence* and *apposition* in their relation to concrescence, I have felt free to use each term in the sense that seems to me the most appropriate.

There remains a more problematical phase of concrescence which has been studied in various vertebrates, and which I have recently investigated in the amphibian embryo. The question involved is this: during the process of overgrowth of the yolk by the dorsal lip of the blastopore, is material dorsal to the blastopore carried from both sides toward the median line? In other words, is there a confluence of material in the median line of that part of the embryo that is formed by overgrowth

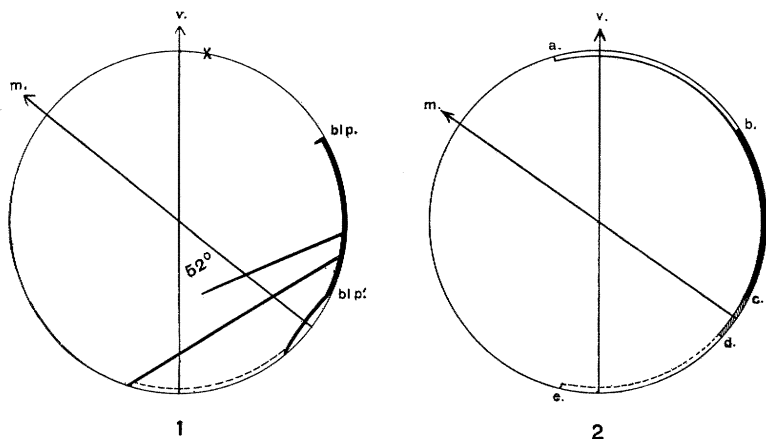


FIG. 1. Diagram showing in lateral view successive positions of the blastopore in the gastrula of *Cryptobranchus alleghehiensis*. *blp.* and *blp'.* respectively indicate early and late positions of the dorsal lip of the blastopore; *m* is the morphological axis of the egg, and *v* the vertical axis determined by gravity. The cross indicates the position of the anterior end of the neural groove.

FIG. 2. Diagram showing in lateral view the position of the embryonic body, and illustrating some features of embryo-formation, in the egg of *Cryptobranchus alleghehiensis*. *a* to *b* (72°), the portion of the embryo formed in situ; *b* to *c* (60°), the portion of the embryo formed by overgrowth of the dorsal lip of the blastopore; *c* to *d* (about 16°), portion formed by convergence of the lateral and ventral lips of the blastopore; *d* to *e* (60°), distance travelled by the ventral lip of the blastopore. Other lettering as in the preceding figure.

and in-turning of the dorsal lip of the blastopore? The problem as concerns the egg of *Cryptobranchus* may be more clearly pointed out with the aid of the accompanying figures (Figs. 1 and 2). In Fig. 1 the transverse lines indicate successive positions of the blastopore, viewed from the lateral aspect. In Fig. 2 the relative amounts of the embryo formed in different ways are represented: about 72° of the anterior end of the embryo

is formed in situ, so far as overgrowth and convergence are concerned; about 16° of the posterior end of the embryo is formed by the convergence of material lying in the region of the lips of the blastopore; the remaining middle portion of the embryo, about 60° in extent, is formed in connection with overgrowth by the dorsal lip of the blastopore, with the possibility of confluence. It is the possibility of confluence in this region that we desire to investigate; also some details concerning convergence and the movements of the neural folds.

The concept of concrescence, especially in the earlier stages of its history, has often been assumed to involve the idea of a certain amount of preformation in the parts that are brought together; they must be differentiated as the anlage of definite organs. In the present paper I shall neglect entirely this phase of the problem; the term concrescence is here employed without any implications as to the amount of differentiation in the regions concerned.

II. METHODS AND TECHNIQUE.

Nearly all the previous experimental work on the problem of concrescence has been done by mechanical methods: an injury of some sort has been inflicted on the living egg and the result in later stages noted. The usual mode of procedure has been to prick the egg with a fine needle, making a slight puncture sufficient only to establish a landmark by means of which the movement of materials may be followed.

The present study is an attempt to apply the method of vital staining to the solution of this problem. The advantage of this method is that extensive markings may be made without in the least interfering with the normal course of development. From Goodale ('11) was obtained the idea of using Nile blue sulphate for this purpose. On account of marked differences in the structure of the gelatinous envelopes of the eggs of the two species, the method of applying the stain to the egg of *Cryptobranchus* necessarily differs from that employed by Goodale for the egg of *Spelerpes*.

Nile blue sulphate in aqueous solution of the proper strength produces on the egg or embryo of *Cryptobranchus* a very distinct

spot which will not wash out, and which is not toxic enough to interfere with the normal development. The large size of the egg (from 6 to 7 mm. in diameter), the ease with which it may be removed from its gelatinous envelope, and the entire absence of pigment make it a peculiarly favorable object for staining experiments. From the behavior of the stain in experiments it appears that it does not spread to any perceptible extent by diffusion, and that stained areas are carried from one position to another only by an actual movement of material. A very faint trail may sometimes be left behind a moving spot, but this appears to be due to secondary staining by the vitelline membrane. The stain enables us to determine the direction and amount of the movement of cells, and to distinguish an actual transference of cellular material from a wave movement or undulation.

My results with *Cryptobranchus* do not harmonize with Goodale's ('11) statement that in *Spelerpes* the yolk granules only are stained. In the early cleavage stages of *Cryptobranchus* the micromeres stain distinctly and keep the stain, while the more heavily yolk-laden parts of the egg stain with difficulty and the stain more readily washes out. In later cleavage stages the micromeres stain more intensely than in the early stages, and the neural folds take the stain with even greater intensity. The inference would seem to be that the cytoplasm stains more readily than the yolk.

The method used in applying the stain to the egg of *Cryptobranchus* is as follows: The egg is removed from its gelatinous envelope and placed in water in a Syracuse watch glass. A small drop of strong aqueous solution of Nile blue sulphate is applied to its surface with a fine pipette. After an interval of about half a minute the excess of stain is washed away and sucked up with a clean pipette. On account of the large size of the egg, magnification is not necessary. The under surface of the egg may be viewed by means of a mirror placed under the watch glass; the mirror is far enough away from the egg so that the entire image may be observed at a single view. A lateral view of the egg may be obtained by holding a piece of mirror in a vertical position in the watch glass beside the egg. For purposes of observation it is possible to turn the egg with a camel's hair

brush, and keep it in any desired position on a bed of cotton; but on account of the extreme delicacy of the egg, mechanical manipulation is preferably to be avoided. The drawings used in illustrating this paper were made with the aid of a mirror. A camera lucida was not employed, for the reason that its use requires too much handling of the egg in order to get it in the right position for drawing. Free-hand sketches were made as accurately as possible, and it is believed that they give as faithful pictures as would be the case were they made with a camera.

III. EXPERIMENTS AND OBSERVATIONS.

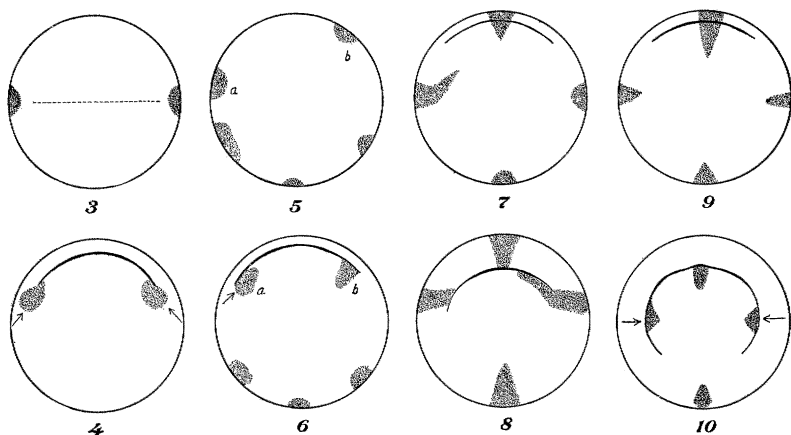
A. Convergence.—In my previous work on the development of *Cryptobranchus* (Smith, '12), observational studies alone gave evidence that a band of cells occupying an equatorial position in the late blastula moves, during gastrulation, toward the vegetal pole and converges on the site of the closing blastopore to form the posterior end of the embryo. By means of staining experiments Goodale ('11) has demonstrated a similar process in the eggs of *Spelerpes* and *Amblystoma*. The following experiments enable us to determine more precisely the nature of this movement and the distribution of the cells involved.

In connection with another series of experiments some eggs were stained in the early first cleavage stage by placing a mark in the equatorial region opposite each end of the cleavage furrow. Figs. 3 and 4 represent one of these eggs in which the first cleavage furrow extended precisely at right angles to the median plane of the future gastrula. In Fig. 4, representing the lower hemisphere of the early gastrula, the two spots have been carried ventrally and posteriorly to a position at the ends of the crescentic blastopore, which they tend to enter from below (*i. e.*, from the posterior side). In comparing these and similar figures it must be remembered that, since the egg is a spherical object and the drawing a projection on a plane surface, the distance through which a mark travels is in certain situations much greater than appears in the drawings.

Fig. 5 represents the lower hemisphere of an egg stained in the equatorial region of the late blastula. Fig. 6, drawn two days later, shows the spots on the posterior side of the egg

appearing entirely below the dorsal lip of the blastopore. They have also moved toward the median line.

Fig. 7 represents the lower hemisphere of an early gastrula stained in the equatorial region in such a way that one of the spots extends in a meridional direction across the dorsal lip of the blastopore. The results two days later (Fig. 8) demonstrate overgrowth and convergence.

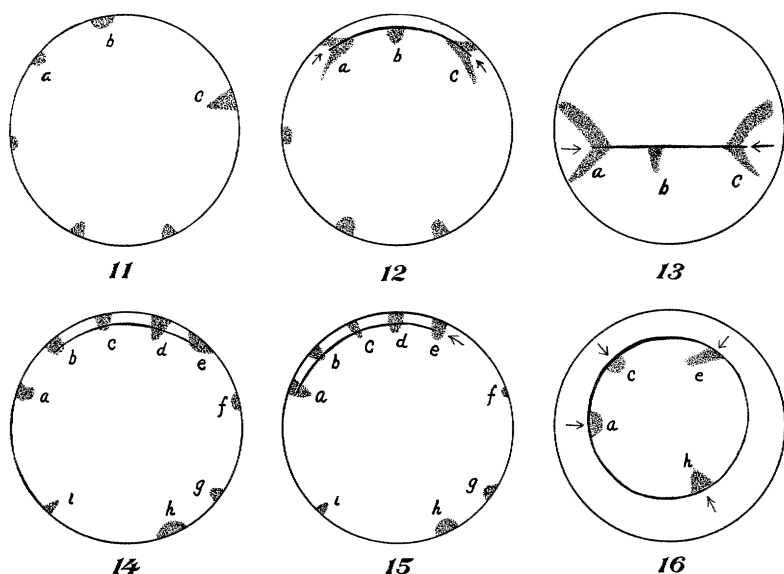


FIGS. 3 TO 10. Each vertical pair of figures represents the history of an individual egg of *Cryptobranchus allegheniensis*. The dotted areas indicate spots produced with Nile blue sulphate. Fig. 3, lower hemisphere of an egg in the first cleavage stage, sketched immediately after marking in the equatorial region opposite the ends of the cleavage furrow. The dotted line indicates the position of the first cleavage furrow which is confined to the upper hemisphere. Fig. 4, lower hemisphere of the same egg sketched a week later in the early gastrula stage. Fig. 5, lower hemisphere of an egg in a late blastula stage sketched immediately after marking in the equatorial region. Fig. 6, lower hemisphere of the same egg, sketched in the early gastrula stage four days later. Fig. 7, lower hemisphere of an egg in the early gastrula stage, sketched immediately after marking in the equatorial region. Fig. 8, lower hemisphere of the same egg sketched two days later. Fig. 9, lower hemisphere of an egg in the early gastrula stage, sketched immediately after marking in the equatorial region. Fig. 10, lower hemisphere of the same egg sketched three days later.

Fig. 9 represents an egg treated in approximately the same manner as the one shown in Fig. 7. This egg sketched three days later demonstrates the in-turning of a large area of the former dorsal lip of the blastopore, and shows more clearly than the preceding the phenomena of convergence. In addition it shows that convergence involves, not merely the lips of the blastopore itself,

but a broad zone of cells occupying the lateral margin of the yolk plug.

Fig. 11 represents the lower hemisphere of an egg stained in the equatorial region of the late blastula. The stained areas are elongated in a meridional direction. Figs. 12 and 13 show the condition two days later. At the level of the early blastopore there is a pronounced shifting of material from each side toward the median line.



FIGS. 11 TO 16. Each horizontal row of figures represents the history of an individual egg of *Cryptobranchus allegheniensis*. The dotted areas indicate spots produced with Nile blue sulphate. Fig. 11, lower hemisphere of an egg in a late blastula stage, sketched immediately after marking in the equatorial region. Fig. 12, lower hemisphere of the same egg sketched in the early gastrula stage, two days later. Fig. 13, same as the preceding, posterior view. Fig. 14, lower hemisphere of an egg in an early gastrula stage, sketched immediately after marking in the equatorial region. Fig. 15, lower hemisphere of the same egg, sketched a day later. Fig. 16, lower hemisphere of the same egg sketched two days later than the preceding.

Fig. 14 represents the lower hemisphere of an egg stained in the equatorial region of the early gastrula; some of the spots extend in a meridional direction across the blastopore. Fig. 16, sketched three days later, shows marked overgrowth and in-

turning on all sides of the yolk plug and particularly on the dorsal side. In addition this figure shows that convergence involves a zone of cells occupying the ventral as well as the lateral margin of the yolk plug. This figure in connection with Fig. 10 shows that the movement of the ventral margin occurs considerably later than the movement of the lateral margin—a result correlated with the delayed development of the ventral lip of the blastopore.

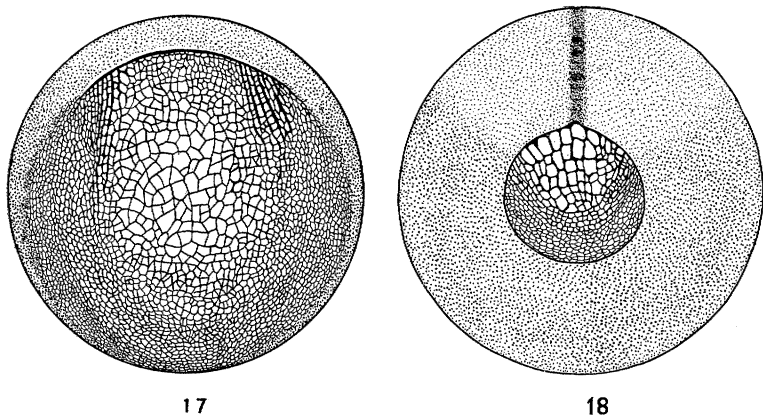


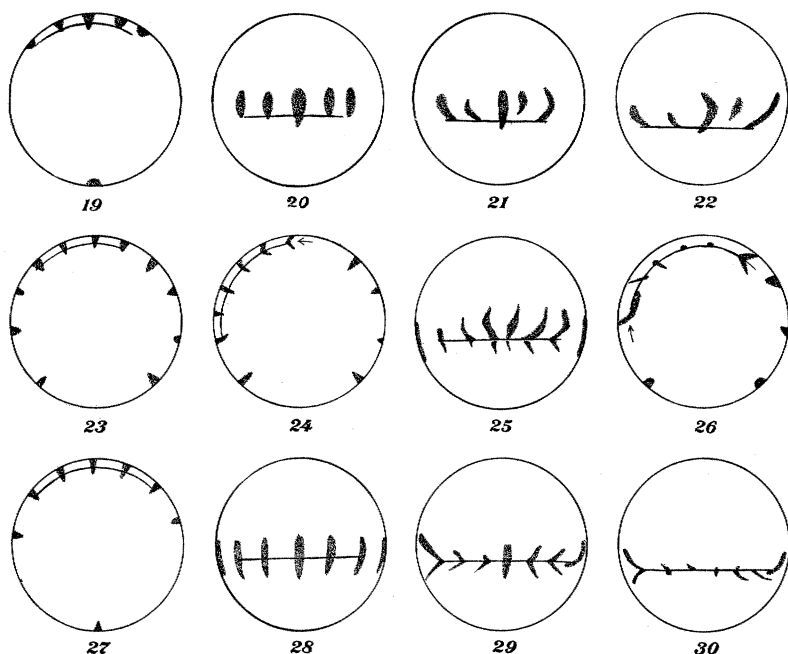
FIG. 17. Lower hemisphere of an early gastrula of *Cryptobranchus allegheniensis*, showing cell outlines. $\times 7$.

FIG. 18. Posterior view of an embryo of *Cryptobranchus allegheniensis* in the neural groove stage, showing cell outlines in the yolk plug. $\times 7$.

Figs. 17 and 18 show that the cells occupying the lateral and ventral margins of the yolk plug, which figure so conspicuously in these movements, are readily distinguishable from the larger yolk cells on the one hand, and the smaller cells of the lips of the blastopore on the other; these marginal cells are arranged in the form of a crescent. We have shown that the marginal cells are the descendents of cells that formed a band in the equatorial region of the late blastula, and it may be here stated that these equatorial cells were of a transitional character, intermediate in size between micromeres and macromeres.

B. Confluence.—The experimental study of the movement of material in the region of the dorsal lip of the blastopore aims to determine (a) whether movements other than overgrowth and in-turning occur in the dorsal lip of the blastopore, and (b) if

such movements occur, can they be explained as a mechanical necessity in the process of invagination and epiboly? My earlier observations (Smith, '12) gave no clue to the occurrence of confluence in this region, so that I approached the experimental



FIGS. 19 TO 30. Each horizontal row of figures represents the history of an individual egg of *Cryptobranchus allegheniensis*. The dotted areas indicate spots produced with Nile blue sulphate. Fig. 19, lower hemisphere of an early gastrula sketched immediately after marking in the equatorial region, especially above the blastopore. Fig. 20, the same, posterior view. Fig. 21, a posterior view of the same egg, sketched a day later. Fig. 22, posterior view of the same egg sketched a day later than the preceding. Fig. 23, lower hemisphere of an early gastrula sketched immediately after marking in the equatorial region. Fig. 24, a similar view of the same egg sketched a day later. Fig. 25, the same as the preceding, posterior view. Fig. 26, the lower hemisphere of the same egg sketched a day later than the preceding. Fig. 27, lower hemisphere of an early gastrula sketched immediately after marking in the equatorial region. Fig. 28, the same, posterior view. Fig. 29, posterior view of the same egg, sketched a day later than the preceding. Fig. 30, posterior view of the same egg, sketched a day later than the preceding.

study of the subject in a skeptical frame of mind that made the results the more impressive, since they were entirely unexpected.

Figs. 19 and 20 represent an egg stained in the equatorial

region of the early gastrula. Fig. 21, sketched a day later, shows unmistakably that, during the process of overgrowth, material lying immediately dorsal to the blastopore is being carried from both sides toward the median line—a phenomenon which I have called “confluence.” Fig. 22, sketched two days later than the preceding, shows the same process carried further, with the complication that the upper ends of the most laterally situated marks are being carried downward and even slightly outward through being involved in the process of convergence. The outward movement is more readily comprehensible if we compare the homologous regions in the embryos of an elasmobranch and a teleost.

Figs. 23 to 26 represent the history of another egg stained in the same manner as the preceding. The latest stage figured shows incidentally that overgrowth is accompanied by extensive in-turning of the dorsal lip of the blastopore. The results as regards confluence are even more striking; but the figures give some evidence of a similar tendency in the material immediately ventral to the early blastopore—that is, in the future yolk plug. This latter fact must be considered in our interpretation of the movement of material in the dorsal lip.

Figs. 27 and 28 represent an egg stained in the equatorial region of the early gastrula in such a manner that the stain extends in a meridional direction across the blastopore, considerably further than in the preceding figures. The result in later stages (Figs. 29 and 30) shows conclusively that the shifting of tissues toward the median line just below the blastopore is almost the mirrored image of that above the blastopore; the differences in the two levels at the ends of the blastopore are to be explained as due mainly to the process of convergence.

These results suggest a mechanical explanation of confluence. Does the material immediately above and below the blastopore merely follow the law of liquids flowing through an orifice, converging toward the point of least resistance? To test the matter I studied the currents produced in shallow water which was allowed to escape from a pan through a slit cut in the bottom. When the slit was made slightly wider at the middle than at the ends, the currents showed a tendency to converge, as shown

in Fig. 31. In the blastopore of *Cryptobranchus*, the point of least resistance would naturally be at the center, where the invagination is deepest. But in comparing Fig. 31 with the preceding figures such as Figs. 25 and 29 one should remember that the stained areas do not represent the actual paths of moving particles—such paths are in reality much more oblique, as will be seen by comparing the original position of the stained areas. There is room for doubt if a mechanical explanation of confluence is really adequate to explain the extreme obliquity of the course taken by individual cells.

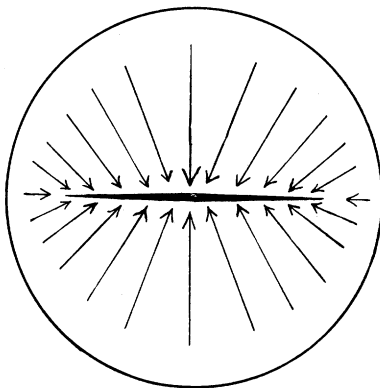
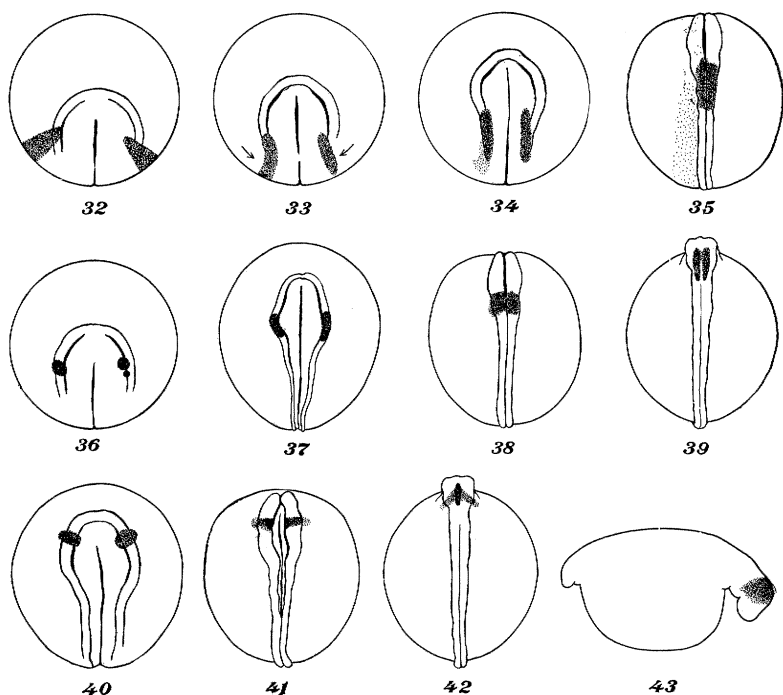


FIG. 31. Diagram showing the direction of the currents in water contained in a shallow vessel and allowed to escape through a slightly elliptical slit in the bottom.

C. The Movements of the Neural Folds.—We have spoken of the movement of the neural folds as a phase of concrecence in its widest sense; in this connection it may be worth while to examine into the character of this movement. Is it a mere wave-like undulation progressing from the lateral margins of the neural plate toward the median line, or is it a movement of translation whereby material is actually carried toward the median line? The study of transverse sections of a series of embryos inclines one to the latter view, and experiments prove conclusively that this view is correct. My results in general agree with and extend those of Goodale ('11) on *Spelerpes*.

Figs. 32 to 35 represent the history of an egg marked in the early neural groove stage. The distance through which material is brought from either side to the median line is remarkable, and

in the absence of experimental demonstration would hardly be suspected. The neural folds, except their most anterior portion, are formed from material lying originally at least 90° apart, or one fourth the circumference of the egg. The forward movement



FIGS. 32 TO 43. Each horizontal row of figures represents the history of an individual egg of *Cryptobranchus allegheniensis*. The dotted areas represent marks made with Nile blue sulphate. Fig. 32, upper hemisphere of an egg in an early neural fold stage, sketched immediately after marking. Fig. 33, upper hemisphere of the same egg sketched a day later. Fig. 34, upper hemisphere of the same egg sketched a day later than the preceding. Fig. 35, dorsal aspect of the same embryo sketched a day later than the preceding. Fig. 36, upper hemisphere of an egg in an early neural fold stage, sketched immediately after marking. Fig. 37, dorsal aspect of the same embryo sketched two days later. Fig. 38, dorsal aspect of the same embryo sketched a day later than the preceding. Fig. 39, dorsal aspect of the same embryo sketched a day later than the preceding. Fig. 40, dorsal view of an embryo in the neural fold stage, sketched immediately after marking. Fig. 41, dorsal aspect of the same embryo, sketched a day later. Fig. 42, dorsal aspect of the same embryo sketched a day later than the preceding. Fig. 43, lateral aspect of the same embryo sketched three days later than the preceding. Four eggs were used for this experiment, with results so nearly identical that the history of any one of these eggs might be represented by Figs. 40 to 43.

of the stained areas is apparent rather than real, since it is due to the rotation of the entire egg on a horizontal axis.

Figs. 36 to 43 require no explanation other than that given in the legends.

The large number of experiments performed to demonstrate the movement of the neural folds gave remarkably uniform results, and clearly indicate that the movement is one of translation, and not a mere wave movement or undulation.

In distinction from the forms of concrecence more intimately related to gastrulation, the mode of concrecence of the neural folds and the gastral mesoderm might be distinguished as concrecence by apposition.

IV. DISCUSSION.

In this paper the term concrecence has been employed in a wider sense than is usual in vertebrate embryology. One's views as to the scope of the term concrecence will naturally depend on his general theory concerning the origin of concrecence; on the other hand that theory is the most acceptable that gives a valid explanation of the largest number of facts, thus bringing them into a common category. The theoretical interpretation that appeals most strongly to the writer is the one stated by Wilson ('90). As the volume containing this contribution is scarce and almost inaccessible to many readers, a résumé of the most important points bearing on this problem is here given.

There are two views as to the significance of concrecence. According to the first view concrecence is a cœnogenetic phase of development; the embryo is temporarily bisected by the yolk, and the two parts afterwards brought together. Concrecence is thus a process of restoration, by which the two halves of the embryo, which have been mechanically separated by the yolk, are united. According to the second view concrecence has a far deeper meaning, and is palingenetic, though the accumulation of yolk may have modified its character. The second view is the one favored by Wilson, and requires further explanation.

The origin of concrecent growth is to be sought in the origin of bilaterality itself—an inquiry which leads us to the problem concerning the origin of bilateral animals from the cœlenterates,

which by common consent are considered to have been their progenitors.

In the higher animals the gastrula stage is regarded as the embryonic representative of the radial, two-layered ancestral type; the blastopore is the representative of the single opening or so-called mouth of the cœlenterate.

Bilateral animals have arisen from radiate forms by the elongation of one of the transverse axes of the latter, the oral face becoming the ventral aspect, and the aboral face the dorsal aspect (this relation is reversed in the vertebrates). The mouth, meanwhile, shifted its position so as to lie near the anterior extremity of the new long axis, and the lateral portions, growing together more or less completely along the region formerly occupied by the mouth, gave rise to the process of concrescence in the ontogeny.

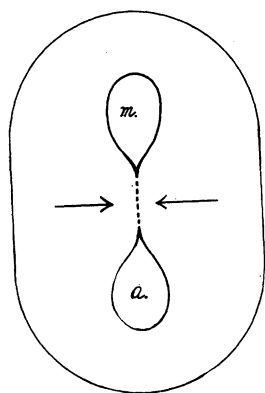


FIG. 44. Diagram showing the mode of blastopore closure in *Peripatus*.

What, then, was the origin of the anus in bilateral animals? In different embryos we find that the blastopore gave rise, sometimes to the mouth (through the persistence of the anterior part of the blastopore, as in the earthworm), sometimes to the anus (through the persistence of the posterior part of the blastopore, as in many vertebrates), and rarely to both (as in *Peripatus*, where the elongated blastopore closes in the middle). The only possible interpretation of these facts would seem to be that the blastopore originally gave rise to both mouth and anus. The case of

Peripatus (Fig. 44) is then an interesting and apparently isolated remnant of the ancestral mode of development, or perhaps a reversion to it. It is interesting to note that in *Peripatus* the two halves of the body are quite well differentiated independently on the two sides of the blastopore; later, these two halves are brought together.

Concrescence is then a **sequence of the closure** of the blastopore, which primitively extended the whole length of the embryo,

the anterior end forming the mouth. The separation of the two sides of the embryo, shown in the vertebrates most clearly in the early history of the mesoderm and the nervous system, was primitively caused by the blastopore itself. In the great majority of cases the original mode of closure of the blastopore has been secondarily modified, but the mesoderm and the neural cords or folds still follow the original mode of development, being laid down separately on either side of the region of the primitive blastopore, and growing together along its line of closure (concrecence by apposition). In cases where the region of the blastopore is occupied by a large mass of yolk, the process of concrecence is much modified and exaggerated; to this extent only, concrecence is to be regarded as a cœnogenetic character.

Taking up now, in the light of this theory, our special problem of concrecence in the vertebrates, we may note that there is no valid objection to the extension of the theory to cover the vertebrates on the ground that forms like *Peripatus* and the earthworm are not ancestral to the vertebrates; granting that these forms are probably far removed from the ancestral line of the vertebrates, we may still rely on the fact of common descent from the cœlenterates. Further, we may note that the ancestral mouth of the vertebrates has been lost, and a new one acquired; the anus represents typically the posterior remnant of the primitive blastopore. Wipe out the upper half of the figure showing blastopore closure in the embryo of *Peripatus* (Fig. 44), and we have left substantially the conditions found in the late gastrula of *Cryptobranchus*. If we give a phylogenetic interpretation to the confluence of materials in the dorsal lip of the amphibian blastopore, then this confluence is but a vestige of the more pronounced shifting of tissues that caused the constriction of the primitive blastopore. The observed confluence of materials in the dorsal lip of the blastopore is such as this theory of concrecence would lead us to expect. I have suggested a possible mechanical explanation, which seems not wholly adequate. The facts are not inconsistent with the palingenetic theory of concrecence.

The process which I have called convergence is necessitated by the large mass of yolk which greatly delays the completion of the process of gastrulation.

Like most phylogenetic speculations, the palingenetic theory of concrescence is weak in that it seems incapable of absolute demonstration. On the other hand the theory is useful in that it brings together in a single view a number of very important anatomical and embryological facts, putting them in an intelligible relation to one another. If we reject this theory, then we can scarcely consider the term concrescence to cover the behavior of the neural folds and the mesoderm in the vertebrates; concrescence becomes limited to events concerned with the present process of gastrulation, and probably applies only to the formation of the posterior end of the embryo. If we accept this theory, then concrescence has a broader and deeper meaning, and explains the most fundamental events in the formation of the embryo.

Perhaps the greatest gain that has come from the theory or theories of concrescence is that research has thereby been stimulated, with the result that we now have a much more accurate knowledge of the early stages of development of many forms than would otherwise be the case. The facts thus brought to light may be of greater value when considered from an altogether different angle, in the development of the various aspects of embryological science.

V. SUMMARY.

By the method of vital staining the following facts concerning the formation of the embryo of *Cryptobranchus* were established: (1) A band of cells occupying the lateral and ventral parts of the equatorial region of the late blastula, during gastrulation comes to occupy the corresponding parts of the margin of the yolk plug, and converges on the site of the closing blastopore. (2) During gastrulation there is a confluence of material lying in the region of the dorsal lip of the blastopore: in connection with the process of overgrowth and in-turning of the dorsal lip of the blastopore, this material shifts from either side toward the median line. (3) The movement of the neural folds is a movement of translation, not a mere wave movement; the neural folds include material originally situated at least 90° apart, which is thus brought into apposition in the median line.

The bearing of these facts on the theory of concrecence is discussed.

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